Plant community dynamics in arid lands: the role of desert ants

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Abstract: Ants (Formicidae, Hymenoptera) play an important role in seed bank, seedling establishment and plant composition of arid ecosystems. Thus, knowing plant-ant interaction provides useful information for managers to design restoration and conservation plans. In this study, the roles of desert harvester ants (*Messor intermedius* and *Messor melancholicus*) and scavenger ants (*Cataglyphis nodus* and *Lepisiota semenovi*) on plant communities were investigated in arid ecosystems of southeastern Iran. Two vegetation types were distinguished in the study area and the nest density of ant species was determined. Furthermore, plant composition and soil seed bank were estimated at different distances from the ant nests. Results showed that the density of *M. intermedius* and *M. melancholicus* nests was higher in dwarf shrub-shrub vegetation type and the density of *C. nodus* and *L. semenovi* nests was higher in dwarf shrub vegetation type. The harvester and scavenger ants had enhanced the seed bank to 55% and 70%, respectively. Therefore, the role of scavenger ants on the plant communities' seed bank was greater than that of harvester ants. Although the scavenger ants were more influential on the annuals and the invasive plant species, the radius impact of the harvester ants on the perennials was greater, i.e., a positive interaction existed between the perennial plants and the harvester ants. *C. nodus* and *L. semenovi* played an important role in enhancing the ecosystem's potential for restoration through establishment of pioneer species in early stage of succession. The activity of *M. intermedius* is crucial for the development and maintenance of climax plant communities in arid ecosystems through assisting the plant species' establishment in late stage of succession. It is essential to preserve the diversity of these key ant species for the maintenance and sustainability of shrubs in arid ecosystems.

Keywords: ants; ecological succession; ecosystem; rangelands; shrubs; vegetation

1 Introduction

Arid lands cover 41% of the Earth's surface, inhabited by 38% of the human population (Safriel et al., 2005). These lands are one of the most sensitive and fragile ecosystems on the world. Arid ecosystems have harsh living conditions and vegetation community dynamic in these arid ecosystems is related to many abiotic (Morecroft et al., 2004; Keith et al., 2009; Wang et al., 2019) and biotic factors (Fagundes et al., 2018). Terrestrial animals such as ants are important drivers of vegetation community dynamic through facilitating plants seed survival and germination in stressful environmental conditions such as drought (Nicolai et al., 2008).

Ants are one of the most widespread insects in the soil with high diversity, abundance and social behavior (Frouz et al., 2016), and are considered as key ecosystem engineers in arid ecosystems (Brown et al., 2012). Ecosystem engineers create, maintain and modify habitats by

substantially changing the chemical and physical composition of substrates (Abe and Higashi, 2001). Ants mostly have local and spot influences on ecosystems due to their small size (Veen et al., 2012). They usually bring a large amount of deep soils to the ground surface for nest construction and maintenance. These organisms can excavate any type of soil and create a wide variety of biogenic structures in the ecosystem (Anderson, 1995). Biogenic structures are important because they are drivers of important processes in the soil such as microbial activity, soil formation, organic matter dynamics, water and gas exchange (Lavelle, 1997).

Ant activity beneath the soil is characterized by the appearance of nest mounts (Lafleur et al., 2005). Nesting of ants is one of the small-scale disturbances, which modifies soil resources in the ecosystem (Farji-Brener and Werenkraut, 2015). Meanwhile, physical and chemical properties of ant nests affect the surrounding plant communities positively or negatively (Folgarait, 1998; Luna et al., 2018). Ants can increase organic matter and nutrients of the soil (Wagner and Nicklen, 2010). Sometimes, there is an inverse relationship between the presence of ant nests and nutrient levels (Dostal et al., 2005). The soils around ant nests improve seedlings establishment due to higher concentration of organic matter (Wagner et al., 2004). Ants also help recruitment practices of plant communities with burrowing seed in the soil (Almeida et al., 2019). Storing seeds sometimes have no positive effect on plant communities. In grasslands, for example, buried seeds of shrub species reduce the control effect of prescribed fire on invasive plants, i.e., shrubs (Harrington and Driver, 1995).

There are different kinds of ants in the ecosystem. Harvester ants are adapted to aridity (Eldridge et al., 2020), which usually collect or harvest seeds as their primary food source (de Almeida et al., 2020). *Messor* is one of the most common harvester ant genera in the deserts (Crawford, 1981). These ants usually make large nests and store seeds and plant residuals in their nests (MacMahon et al., 2000). Scavenger ants, which collect dead items, may predate small preys (Way and Khoo, 1992). They are less known than harvester ants in ecological studies (Bestelmeyer and Wiens, 2003). Scavenger ants play an important role in nutrient distribution in arid ecosystems (Bestelmeyer and Wiens, 2003).

Differences in plant and ant attributes affect the ant-plant interactions (Hughes and Westoby, 1990). Dys-zoochory happens when seeds are foraged by animals that store them for winter or accidentally lose them during transport (Vittoz and Engler, 2007). Myrmecochory is a particular case of dys-zoochory, a mutualism interaction in which food resources and services are exchanged and both ants and plants take advantage. Myrmecochorous plants can attract specific ants with varying diet, nest structure, activity time and nest position (Ness et al., 2009), which reciprocally affect the service performance of ants to plant communities (Boulay et al., 2007).

There is no clear evidence of the impacts of ant activities on plant communities and ecosystem function in arid lands (Saha et al., 2012). The interactions between ants and plant species seeds take several forms such as dispersal, predation and parasitism (Penn and Crist, 2018). Harvester ants can negatively and positively influence plant communities through both seed consuming and seed dispersal processes (Arnan et al., 2010). Harvesters have a positive impact on seeds growth due to generating organic-rich microsites in their nests (Ness et al., 2009) and facilitate ecosystem recovering in arid lands (Nicolai et al., 2008). Paolini et al. (2020) indicated that harvester ants as granivores had important impact on restoring invaded sagebrush communities. Harvester ants can annually decline the potential of seed pool in shrub-steppe ecosystems (Crist and MacMahon, 1992). In addition, harvester ants as seed dispersers can redistribute seeds and enhance plant diversity (Wills and Landis, 2018).

Studying the response of plant communities to environmental manipulators such as ants is crucial for better understanding of ecosystem degradation and implementing restoration strategies for arid lands (Wang et al., 2019). The response of plant communities to ant activities is complex due to the interactions between different ant species and plant communities. Therefore, a deep understanding of the roles played by ant species in plant communities is necessary (Wang et al., 2019). Therefore, this study aimed to (1) evaluate the nest density of harvester and scavenger ants in two plant communities, (2) investigate the role of harvester and scavenger ants in driving plant composition, and (3) assess the role of harvester and scavenger nests on soil seed banks and

seedlings establishment in the arid ecosystems.

2 Materials and methods

2.1 Study area

The study area located in the Baqbazm Watershed with an area of 263 km² in southeastern Iran (29°45′–30°00′N, 21°56′–31°56′E; Fig. 1). The mean elevation is 2545 m a.s.l. Mean annual precipitation is 210 mm, which mostly occurs in winter. Mean temperature ranges from 7°C to 26°C. The region is characterized by hot summers and cold winters. There are two main vegetation types in the region: *Artemisia sieberi* (dwarf shrub) and *Artemisia sieberi-Pteropyrum aucheri* (dwarf shrub-shrub) (Table 1). The soils are sandy loam to sandy clay.

There are 4 dominant desert ants in the region: *Messor intermedius* (*M.int*; Santschi, 1927) and *Messor melancholicus* (*M.mel*; Arnol'di, 1977), which are harvester ants, and *Cataglyphis nodus* (*C. nod*; Brullé, 1833) and *Lepisiota semenovi* (*L.sem*, Ruzsky, 1905), which are scavenger ants.
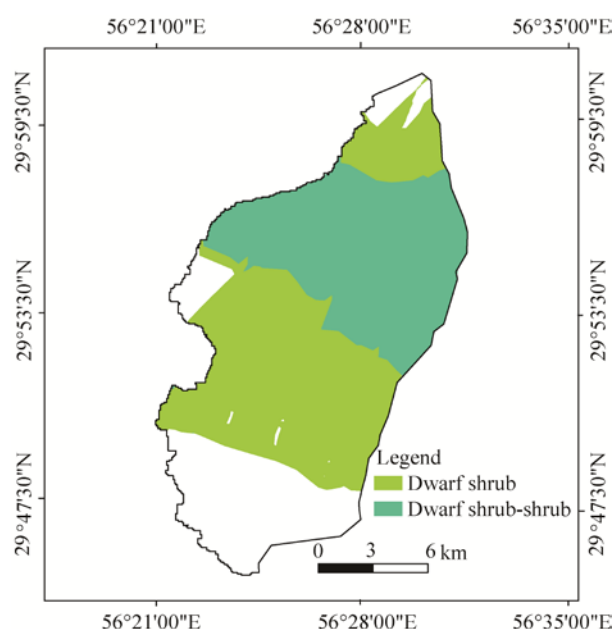

Fig. 1 Location of the study area and vegetation type in the Baqbazm Watershed, Iran. Dwarf shrub is *Artemisia sieberi* and dwarf shrub-shrub is *Artemisia sieberi-Pteropyrum aucheri*.

Table 1 Vegetation type in the Baghbazm Watershed, Iran

Vegetation type	Elevation (m)	Area (km²)	Soil type	Grazing intensity	Dominant plant species
Dwarf shrub	2126	92	Sandy clay	Medium	*Artemisia sieberi*
Dwarf shrub-shrub	2346	112	Sandy loam	Medium	*Artemisia sieberi-Pteropyrum aucheri*

2.2 Data collection

2.2.1 Nest density of ants

Twenty-five plots in 20 m×20 m size were randomly placed in each vegetation type to assess density of mature nests at spring 2019. The number of ant nests in each plot was recorded. We recorded the nests based on ant species and identified through signs such as excavated soil and intensified activities of ants. In each vegetation type, 10 nests (total 80 nests for 4 ant species) and 8 control sites (10 m away from the nest, total 16 plots) were randomly selected for vegetation and soil sampling (Almeida et al., 2019).

2.2.2 Seedling

In 80 plots around nests and 16 control plots, richness and abundance of seedling were measured

by counting the number of seedling (Almeida et al., 2019).

2.2.3 Seed bank

For estimation of soil seed bank, soil samples were taken in late February 2019 before the spring rains and onset of germination. Soil samples were taken within a 20 cm×20 cm quadrat with the depth of 10 cm from 80 nests and 16 control plots. Samples were kept in the dark at temperatures less than 5°C for two weeks (Ter Heerdt et al., 1996). After removing coarse plant parts such as roots and stones, soil samples were separately mixed and spread on the sand substrate in 20 cm×20 cm plastic trays (Sternberg et al., 2003). Seeds were exposed to enough light for seed for three month. Thereafter, seedlings were counted and identified every 12 d (Chaideftou et al., 2009).

2.2.4 Structure of plant communities

Plant attributes (individual number, successional stage, vitality and palatability) were measured in 80 plots around nests and 16 control plots. Visual assessment of crown (crown defoliation, epicormic growth, crown size and the number of dead branches) was used to determine plant vitality (Grimes, 1978). We determined palatability classes for livestock (class I, high palatability; class II, fair palatability; class III, poor palatability) of plant species based on Amiri et al. (2008) and Samadi et al. (2020). Litter percentage was also measured in each plot. We divided plant species into three groups according to their presence in the successional stages: pioneer species, early-successional species and late-successional species (Fagundes et al., 2018). Pioneer species are the first plants that establish in degraded regions; early-successional species establish in degraded regions just after pioneer species; late-successional specie rarely establish in degraded regions (Maia, 2012). We determined invasive plants based on consultation from local experts (Rahman and Roy, 2014).

For each ant species, 5 nests were randomly selected and then canopy cover and number of individual species were measured in 1 m×2 m plots at 0.5, 1.0, 2.0, 3.0, 4.0, 5.0, 10.0 and 15.0 m distances from the nests. Canopy cover of plant species was visually estimated in each plot. Canopy cover was calculated as percentage of the ground surface covered by plants in each plot. In twenty-five 20 m×20 m plots in each vegetation type, we estimated habitat fragmentation using area, pyramid and length of plant patch based on the method of Flowers et al. (2020).

2.3 Data analyses

We measured richness of seedling and plant based on individual numbers of plant species. Shannon's diversity index was calculated as follow:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i , \tag{1}$$

Where H' is the Shannon's diversity index, S is the total number of plant species, p_i is the proportion of the individual number belonging to the ith species (Mbuthia et al., 2012).

Mann-Whitney U test was used to compare vegetation type in terms of nest density of ants (Leal et al., 2007). One-way analysis of variance (ANOVA) and least significant difference (LSD) were used to compare seedling attributes (density, canopy cover, Shannon's diversity index and richness of plant species) in 96 plots (Zar, 1996). General linear model (GLM; Bolker et al., 2009) was used to estimate the most important drivers affecting nest density of ants in the ecosystem. Residual analysis and Akaike information criterion (AIC) were used to assess goodness of fit for models. We treated the plant communities' attributes as predicator (x_1, x_2, ..,) and response (y) variables based on GLM structures (Equation 2; b is the constant).

$$y = b_0 + b_1 x_1 + b_2 x_2 + ... \tag{2}$$

The relationship between plant species and four ant species was investigated using principal component analysis (PCA). Species frequency was analyzed as a function of the interactions between plant species and nest density of four ants under loadings of the two-first PCA axes. PCA was performed with the PC-ORD v4.0 package (McCune and Mefford, 1999). Covariance analysis (ANCOVA) was used to relate the number of pioneer, early- and late-successional species (converted by $\ln(x+1)$; Farji-Brener et al., 2009) to four ant species. In the model, the number of species and the number of variant individuals were considered as dependent variables, and

vegetation types were considered as random variables. Distance from nest, ant type (harvester and scavenger) and ant species were considered as covariates in covariance analysis. Prior to statistical analysis, we used the logarithms of ant nest density and distance from nest to correct the non-linearity between covariate parameters and independent variables. All analyses were performed using SPSS v16.0 statistic software package.

3 Results

Twenty-nine plant species were identified in the region, in which 27%, 27% and 46% of them belonged to pioneer, early- and late-successional species, respectively (Table 2) and 3%, 42% and 55% of them belonged to palatability classes I, II and III, respectively. There was a significant difference between dwarf shrub and dwarf shrub-shrub vegetation types in terms of nest density of ants (Fig 2). Nest densities of *M. intermedius* (12.2 ($\pm$1.76) nest/hm^2) and *M. melancholicus*

Table 2 Plant species, family, life form, palatability class and successional stage in two vegetation types

Plant species	Family	Life form	DSh	DSh-Sh	Palatability	Abbreviation	Successional stage
Aellenia subaphylla (C.A.M.) Botsch	Chenopodiaceae	Ch	*	*	III	*A.sub*	Pioneer
Alhagi camelorum Boiss. et Bh.	Fabaceae	Ch	*		III	*A.cam*	Pioneer
Artemisia sieberi Besser.	Asteraceae	Ch	*	*	II	*A.sie*	Late-successional
Boissiera squarrosa (Banks&Sol.)	Poaceae	Th		*	III	*B.sqr*	Pioneer
Bromus tectorum L.	Poaceae	Th	*	*	III	*B.tec*	Pioneer
Acanthophyllum macrodon Edgew.	Caryophyllaceae	Ch	*		III	*A.mac*	Late-successional
Eruca sativa Miller	Brassicaceae	Th	*	*	III	*E.sat*	Early-successional
Ferula assa-foetida L.	Apiaceae	Hem		*	II	*F.ass*	Late-successional
Peganum harmala L.	Zygophyllaceae	Hem	*		III	*P.har*	Pioneer
Pteropyrum aucheri Jaub .et. Sp.	Polygonaceae	Ph		*	II	*P.auc*	Late-successional
Salsola brachiata Pall	Chenopodiaceae	Th	*	*	III	*S.bra*	Pioneer
Salsola kali L.	Chenopodiaceae	Th		*	III	*S.kal*	Early-successional
Scariola orientalis L.	Asteraceae	Ch	*		III	*S.ori*	Late-successional
Echinops ritrodes Bunge	Asteraceae	Hem	*	*	III	*E.rit*	Early-successional
Launaea acanthodes (Boiss.)	Asteraceae	Ch		*	II	*L.aca*	Pioneer
Zygophyllum fabago L.	Zygophyllaceae	Ph		*	II	*Z.fab*	Late-successional
Gundelia tournefortii L.	Asteraceae	Hem	*		II	*G.tou*	Early-successional
Eremurus persicus (Jaub&Spach)	Liliaceae	Ge	*	*	II	*E.per*	Late-successional
Cousinia nekarmanica Rech.f.	Asteraceae	Th	*	*	III	*C.nek*	Pioneer
Taraxacum roseum Bornm. ex	Asteraceae	Th	*	*	I	*T.ros*	Late-successional
Oryzopsis holciformis (M.Bieb.)	Poaceae	Hem	*		III	*O.hol*	Late-successional
Euphorbia denticulata Lam.	Euphorbiaceae	Th		*	III	*E.den*	Early-successional
Bromus dantoniae Trin.	Poaceae	Th	*	*	III	*B.dan*	Early-successional
Centaurea virgata Lamarck.	Asteraceae	Th	*	*	III	*C.vir*	Early-successional
Nepeta heliotropifolia Lam.	Lamiaceae	Hem	*		II	*N.hel*	Late-successional
Stipa barbata Desf.	Poaceae	Hem	*	*	II	*S.bar*	Late-successional
Noaea mucronata (Forssk.) Asch.& Schweinf.	Chenopodiaceae	Ch		*	III	*N.muc*	Early-successional
Hertia angustifolia (DC.) Kuntze	Asteraceae	Ph	*	*	II	*H.ang*	Late-successional
Stachys inflata Benth.	Lamiaceae	Th	*	*	II	*S.inf*	Late-successional

Note: DSh, dwarf shrub; DSh-Sh, dwarf shrub-shrub; Ch. Chamaephytes; Th, Therophytes; Hem, Hemicryptophytes; Ph, Phanerophyte; Ge, Geophytes. I, II and III indicate high, fair and poor palatability, respectively. The abbreviations are the same as in Figure 3 and Table 4.

(14.31 ($\pm$0.87) nest/hm^2) were higher in dwarf shrub-shrub vegetation type than in dwarf shrub vegetation type (6.87 ($\pm$0.65) and 6.02 ($\pm$0.45) nest/hm^2, respectively). *C. nodus* (19.78$\pm$1.78 nest/hm^2) and *L. semenovi* (14.65 ($\pm$0.95) nest/hm^2) had higher nest density in dwarf shrub vegetation type (Fig. 3).
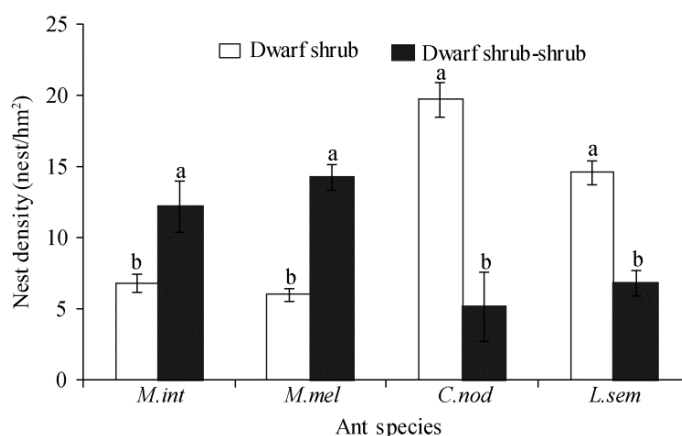

Fig. 2 Nest density of different ant species in two vegetation types. *M.int*, *Messor intermedius*; *M.mel*, *Messor melancholicus*; *C.nod*, *Cataglyphis nodus*; *L.sem*, *Lepisiota semenovi*. Bars are standard deviations. Different lowercase letters indicate significant differences between two vegetation types within the same ant at *P*<0.05 level.
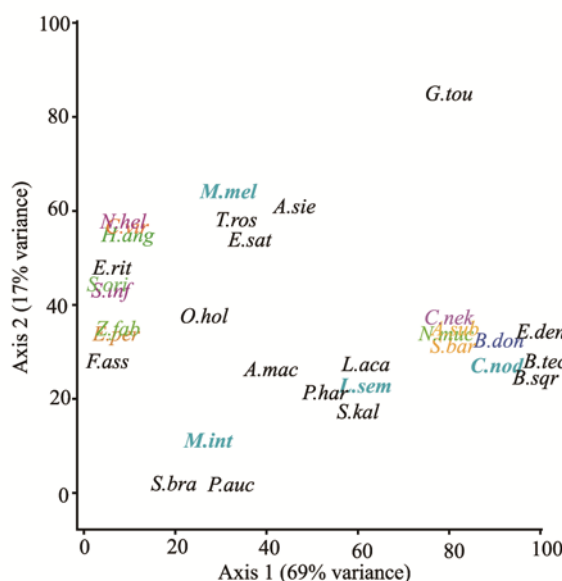

Fig. 3 Distribution of plant species, and harvester and scavenger ants along two first axes of principal component analysis (PCA). *M.int*, *Messor intermedius*; *M.mel*, *Messor melancholicus*; *C.nod*, *Cataglyphis nodus*; *L.sem*, *Lepisiota semenovi*.

Four ant species increased seedling density, canopy cover, Shannon's diversity index and richness compared with control sites (Table 3, *P*<0.05). The highest seedling density (1.79 ($\pm$0.88) individuals/m^2) and canopy cover (24.81% ($\pm$2.60%)) were observed around nests of *M. intermedius*. The highest Shannon's diversity index (1.42 ($\pm$0.86)) and richness (8.26 ($\pm$1.69)) were related to *M. melancholicus* and *L. semenovi* nests. The results confirmed that ants increased seedling density in the soil. *A. sieberi* that included the highest density of seed bank had more seed abundance around nests of *M. intermedius* (Table 4).

Table 3 Density, canopy cover, Shannon's diversity index and richness of seedlings near ant nests and control site in two vegetation types

Vegetation type	Ant nests and control site	Density (individuals/m²)	Canopy cover (%)	Shannon's diversity	Richness
Dwarf shrub	*L.sem*	0.73±0.64[a]	10.40±1.69[a]	0.82±0.81[a]	7.42±3.63[a]
	C.nod	0.61±0.34[a]	9.76±1.24[a]	0.70±0.63[a]	6.50±4.72[a]
	M.int	0.95±0.68[b]	24.81±2.60[b]	1.38±0.85[b]	5.43±2.69[a]
	M.mel	0.82±0.72[a]	17.30±2.60[b]	1.42±0.86[b]	5.63±3.75[a]
	Control	0.49±0.33[c]	2.73±1.64[c]	0.43±0.35[c]	3.21±1.73[b]
Dwarf shrub-shrub	*L.sem*	0.86±0.47[a]	11.27±1.61[a]	1.40±0.59[a]	8.26±1.69[a]
	C.nod	0.72±0.35[a]	11.47±0.23[a]	0.93±0.43[b]	6.40±6.39[a]
	M.int	1.79±0.88[b]	15.23±2.16[b]	0.82±0.39[b]	6.12±3.19[a]
	M.mel	1.12±0.65[b]	14.57±3.59[b]	0.74±0.69[b]	5.42±2.79[a]
	Control	0.48±0.31[c]	3.23±2.74[c]	0.40±0.29[ac]	2.21±1.35[b]

Note: Mean±SD. Different lowercase letters indicate significant difference among different sites within the same vegetation type at $P<0.05$ level. *L. sem*, *Lepisiota semenovi*; *C.nod*, *Cataglyphis nodus*; *M.int*, *Messor intermedius*; *M.mel*, *Messor melancholicus*.

Table 4 Density of seed bank near ant nests and control site in two vegetation types

Plant species	Dwarf shrub-shrub (individuals/m²)					Dwarf shrub (individuals/m²)				
	L.sem	*C.nod*	*M.int*	*M.mel*	Control	*L.sem*	*C.nod*	*M.int*	*M.mel*	Control
A.sub	0.3±0.1	0.0	0.8±0.6	0.5±0.2	0.0	0.7±0.2	1.8±0.7	1.7±0.6	0.0	0.0
A.cam	1.3±1.2	1.6±1.3	0.0	0.0	0.6±0.3	0.7±0.4	0.6±0.3	0.0	0.0	0.0
A.sie	4.1±3.5	2.7±1.1	6.8±4.4	5.3±0.1	1.3±0.7	8.2±2.1	8.3±2.8	11.3±10.7	9.5±8.4	3.3±2.8
B.sqr	2.3±1.1	1.5±1.3	0.8±0.6	0.0	0.3±0.2	3.4±2.5	2.1±1.6	0.0	0.0	0.4±0.3
B.tec	1.4±1.6	1.5±0.7	0.5±0.3	0.0	0.0	1.8±1.2	1.4±0.7	0.0	0.0	0.7±0.4
A.mac	0.0	0.5±0.1	1.2±0.6	0.5±0.3	0.3±0.1	0.0	0.0	2.1±1.7	1.3±1.2	0.0
E.sat	0.6±0.1	0.0	0.0	0.0	0.0	0.0	0.4±0.1	0.0	0.0	0.0
F.ass	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0. 6±0.1	0.0	0.0
P.har	0.6±0.3	0.5±0.2	0.0	0.0	0.0	0.0	0.8±0.2	0.0	0.0	0.6±0.4
P.auc	0.7±0.2	0.6±0. 4	4.5±1.3	2.6±1.2	0.5±0.2	0.0	0.0	0.0	0.0	0.0
S.bra	0.4±0.3	0.0	0.0	0.0	0.0	1.3±0.9	0.8±0.5	0.0	0.0	0.5±0.4
S.kal	0.0	0.3±0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S.ori	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3±0.8	0.9±0.6	0.0
E.rit	0.8±0.6	0.0	0.0	0.0	0.0	1.3±0.7	1.2±0.6	0.0	0.0	0.6±0.5
L.aca	0.0	0.0	0.0	0.0	0.0	0.3±0.1	0.5±0.2	0.0	0.0	0.0
Z.fab	0.0	0.0	0.9±0.2	0.0	0.0	0.0	0.0	1.8±1.3	1.3±1.1	0.7±0.5
G.tou	0.4±0.3	0.6±0.4	0	0.0	0.6±0.2	0.0	0.8±0.4	0.0	0.0	0.0
E.per	0.0	0.0	0.6±0.2	0.3±0.1	0	0.0	0.0	0.4±0.3	0.0	0.0
C.nek	0.4±0.2	0.5±0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
T.ros	0.0	0.6±0.2	0.0	0.5±0.4	0.0	0.0	0.6±0.2	0.0	1.4±0.6	0.4±0.2
O.hol	0.4±0.1	0.5±0.3	0.0	0.0	0.3±0.2	0.8±0.2	0.6±0.4	0.0	0.0	0.0
E.den	0.7±0.3	0.6±0.2	0.0	0.0	0.2±0.1	0.0	0.3±0.1	0.0	0.0	0.5±0.2
B.dan	0.0	0.0	0.0	0.0	0.4±0.1	0.0	0.0	0.0	0.0	0.0
C.vir	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6±0.3	0.0	0.5±0.3
N.hel	0.0	0.0	0.5±0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S.bar	0.0	0.0	0.8±0.7	0.0	0.0	0.0	0.7±0.3	0.2±0.1	0.0	0.8±0.6
N.muc	0.0	0.3±0.1	0.0	0.0	0.0	0.6±0.5	0.0	0.0	0.0	0.0
H.ang	0.0	0.0	0.8±0.7	0.6±0.3	0.0	0.0	0.0	0.9±0.3	0.7±0.4	0.5±0.2
S.inf	0.0	0.0	0.0	0.0	0.0	0.0	0.7±0.4	0.8±0.6	0.0	0.0

Note: mean±SD. *L. sem*, *Lepisiota semenovi*; *C.nod*, *Cataglyphis nodus*; *M.int*, *Messor intermedius*; *M.mel*, *Messor melancholicus*.

About 69% and 17% of variations were explained by the two first axes of PCA. The cumulative variance explained by these two axes was 86%. Plant species distribution along the two first axes of PCA showed that pioneer and early-successional plant species such as *Bromus tectorum*, *Boissiera squarrosa*, *Aellenia subaphylla*, *Launaea acanthodes* and *Salsola kali* are associated with ants *C. nodus* and *L. semenovi* and most late-successional plant species such as *Artemisia sieberi*, *Pteropyrum aucheri*, *Stipa barbata* and *Ferula assa-foetida* are associated with *Messor* ants (Fig. 4).
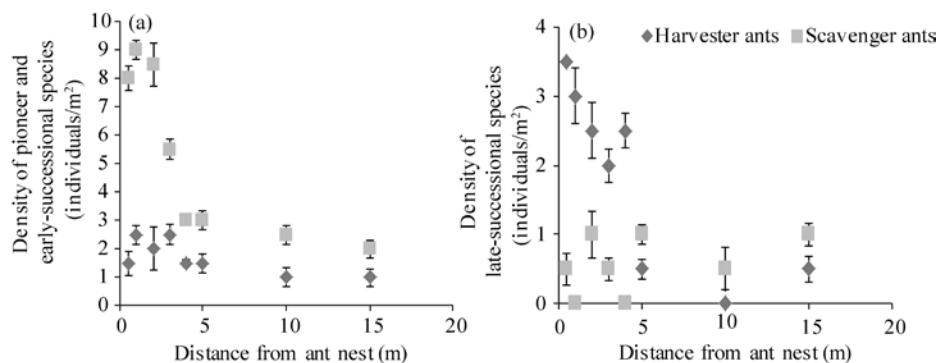

Fig. 4 Density of pioneer, early- (a) and late-successional (b) species in different distances from nests of harvester and scavenger ants. Bars indicate standard deviations.

GLM result revealed the relationship between structural attributes of plant communities and nest density of four ant species (Table 5). Plant palatability and seed bank were significantly related to nest density of *Messor* ants. Abundance of invasive plants had a significant relationship with nest density of *C. nodus* and *L. semenovi*. Plant species life form, diversity and richness were positively linked to nest density of four ant species and habitat fragmentation was negatively linked to nest density of four ant species (Table 5).

Table 5 Result of generalized linear model (GLM) for the relationship between ecosystem structural attribute and density of four ant species

Item	*L.sem*	*C.nod*	*M.int*	*M.mel*
Plant attribute	AIC=345.67; Residual deviance=476.4	AIC=452.97; Residual deviance=408.3	AIC=397.23; Residual deviance=312.8	AIC=492.74; Residual deviance=438.1
Palatability	1.03[ns]	2.43[ns]	37.98**	26.65**
Life form	5.32*	5.21*	7.23*	6.23*
Abundance of invasive plants	7.23*	14.12**	1.23[ns]	1.65[ns]
Vitality	2.34[ns]	6.23*	23.43**	13.23**
Habitat fragmentation	−16.23**	−21.32**	−58.23**	−32.12**
Seed bank	5.23*	5.47*	1.15[ns]	0.79[ns]
Litter	6.53*	7.53*	6.14*	2.13[ns]
Species diversity	12.12**	13.32**	4.32*	5.23*
Species richness	5.13*	6.32**	5.23*	5.12*

Note: AIC, Akaike information criterion; * and ** are significances at $P<0.05$ and $P<0.01$ levels, respectively. ns, non-significance. *L. sem*, *Lepisiota semenovi*; *C.nod*, *Cataglyphis nodus*; *M.int*, *Messor intermedius*; *M.mel*, *Messor melancholicus*.

ANCOVA showed that there was no significant relationship between vegetation type and richness of pioneer, early- and late-successional species. Ant nest attributes was significantly related to richness of pioneer, early- and late-successional species (Table 6). Richness and abundance of pioneer, early-successional species were significantly related with distance from nest and ant type. There were significant relationships between richness and abundance of late-successional species and distance from nest, type and nest density (Table 6). Vegetation type and their interaction with covariant had no effect on the number of nests and the number of species at different successional stages. Results showed that the density of late-successional

species increased with distance from harvester ant nests and there was no significant relationship between the density of pioneer and early-successional species with distance from harvester ant nests. The density of pioneer and early-successional species decreased with distance from scavenger ant nests (Fig. 4).

Table 6 Results of ANCOVA (covariance analysis) for vegetation type, log nest density, ant type and log distance from nest in pioneer, early- and late-successional species

Item	Pioneer and early-successional species				Late-successional species			
	Species		Nest		Species		Nest	
	F	P value	F	P value	F	P value	F	P value
Vegetation type	0.15	0.854	0.11	0.892	2.82	0.101	2.12	0.231
Log distance from nest	5.85	0.003	16.87	0.000	12.32	0.000	17.26	0.000
Log nest density	3.98	0.043	2.20	0.107	4.65	0.005	4.13	0.006
Ant type	29.79	0.000	13.85	0.000	25.65	0.000	18.85	0.000
Log distance from nest×Log nest density	1.34	0.432	0.87	0.532	1.65	0.321	1.76	0.316
Log distance from nest×Ant type	18.43	0.000	14.72	0.000	21.76	0.000	15.76	0.000
Vegetation type×Log distance from nest	0.56	0.734	0.43	0.768	1.86	0.321	2.65	0.212
Vegetation type×Log nest density	0.02	0.987	0.11	0.893	1.12	0.476	1.16	0.453
Vegetation type×Ant type	2.76	0.123	2.16	0.236	1.43	0.412	1.54	0.328

4 Discussion

Ants are social insects of the family Formicidae and belong to the order Hymenoptera. Soil is one of their most important habitats. Ants act as ecosystem engineers and have a great impact on the physical, chemical and biological properties of the soil. Ants play a key role in arid ecosystems. Ant nests are not uniquely distributed in vegetation. Ants improved seed bank and accelerated ecological succession in plant communities in our study region. Scavenger ants could drive pioneer and early-successional species and harvester ants could help late-successional species to establish in arid ecosystems.

4.1 Ants, seedling establishment and seed bank

The diversity and density of seed banks in sites near ant nests were higher than those of control sites, which is consistent with other studies (Leal et al., 2007; Inés et al., 2014). Some studies indicated that the negative impacts of ants on seed bank in desert areas are related to foraging behavior and seed consumption of ants (Costa et al., 2008; Pirk and de Casenave, 2014). Harvester and scavenger ants respectively had positive effects on seed densities of 55% and 70% of plant species in seed bank. The effect of scavenger ants on seed bank was greater than that of harvester ants in our study region. However, Levine et al., (2019) reported that harvester ants had a more effective role on seed dispersal than scavenger ants. Scavenger ants are a common species distributed in arid ecosystems (Espadaler and Gomez, 1996). Dead insects are the staple food of scavenger ants, but they also collect seeds on soil surface (Pfeiffer et al., 2010). The *Cataglyphis* and *Lepisiota* ants, which are nature's cleaners, had a greater impact on seed bank of annual grasses and plant species with small-sized seeds. Annual plants related to *C. nodus* and *L. semenovi* are known to produce a large number of small-sized seeds (Erkkilä and Heli, 1998). Hence, seed bank in arid ecosystems was significantly related with nest density of *C. nodus* and *L. semenovi* compared with *Messor* ants. Nest density of *Messor* ants was higher in dwarf shrub-shrub vegetation type, which includes plant species producing larger seeds (*Pteropyrum aucheri*). Detrain and Pasteels (2000) pointed out that *Messor* ants prefer larger seeds for foraging. *Messor* ants declined seed density by consuming and foraging seeds in arid ecosystems (Detrain and Pasteels, 2000; Azcárate et al., 2005).

Ants also had positive effects on seed germination and seedling establishment in plant communities. Contrary to the results of seed bank, harvester ants were more successful in

seedling establishment than scavenger ants. Ant nests improved seedlings growth by promoting habitat conditions for plant growth (Moutinho et al., 2003). Former studied indicated that *Messor* nests had positive impact on the hydrological characteristics of arid lands through improving nutrient cycling (Lei, 2000; Cammerat et al., 2002), which increases the richness and abundance of other soil animals (Ginzburg et al., 2008).

4.2 Relationship between ants and plant community

Different plant species play different roles in the evolution of plant communities (Fagundes et al., 2018). Ants may drive different stages of ecological succession through improving specific plant species. The scavenger ants *C. nodus* and *L. semenovi* were drivers of pioneer species that consume nutrients at a slower rate and survive longer. Pioneer species are evolved resistance to environmental stresses for establishment in arid ecosystems (Grime, 1977). Nests density of ants is a good indicator of the ecosystem potential for restoration (Takahashi and Itino, 2012). The results of this study showed that *C. nodus* and *L. semenovi* can be used to assess the status of arid ecosystems after environmental disturbances. These ants increase the density of pioneer and early-successional species seeds around their nests. The seed bank around these species nests can potentially be used in vegetation restoration (Hopfensperger, 2007). In this study, the density of scavenger ant nests was higher in dwarf shrub vegetation type than dwarf shrub-shrub vegetation type, indicating the higher potential of this vegetation type for restoration. In addition, *Boissiera squarrosa* and *Bromus tectorum* that are invasive plant species, have higher densities around *Cataglyphis* nests. Seeds of annual species usually are ripe at mid-summer. *Cataglyphis* ants are more active at higher temperatures than *Messor* ants (Ruano et al., 2000). *Cataglyphis* ants can collect seeds at a high speed even at the warmest time of the day (Harkness and Wehner, 1977). They are therefore more capable of collecting the seeds of annual plant species. Berg-Binder and Suarez (2012) also showed that ant nests had a positive effect on the establishment and spread of invasive plant species.

Plant species distribution around ant nests showed that there is a significant relationship between late-successional species and nest density of *Messor* ants. Water retention is crucial for the establishment of late-successional species in the ecosystem (Dodson et al., 2014). *Messor* ants help to the establishment of late-successional species by improving water accessibility (Ginzburg et al., 2008). Typically, late-successional species are more sensitive to environmental disturbances (Fagundes et al., 2018). The ants can be very effective in the survival of these species in desert ecosystems by providing a good shelter for seeds during dormancy or against environmental stress (Nicolai et al., 2008). Dormancy has been identified in the seeds of *Pteropyrum aucheri* and seeds buried in the soil have a higher germination rate (Rafiei and Matinkhah, 2013). *Artemisia sieberi* seeds also delay germination for a long time (Jabarzare et al., 2011). Therefore, storing *Artemisia sieberi* seeds by *Messor* ants plays a very important role in the survival of this species.

Our finding showed that the radius impact of harvester ants on late-successional species is up to 4 m from the nest. Brown et al. (2012) concluded that *Messor* ants enhanced dwarf shrub communities in the refuse zone around nests. The radius impact of scavenger ants on early-successional and pioneer species was up to 5 m from the nest. Pioneer and early-successional species related to scavengers can develop very faster than late-successional species in the ecosystem (Fagundes et al., 2018). Late-successional species usually have fewer seeds with larger size. As a result, activity of *Messor* ants is critical for the distribution of these species in the ecosystem. The areas with higher *Messor* ants have more late-successional species than the areas where *C. nodus* and *L. semenovi* are dominant.

However, palatability (higher protein content) is one of the plant attributes that tempts *Messor* ants to harvest seeds. Non-palatable species, such as *Bromus tectorom*, whose seeds have high fiber and low protein contents (Crist and MacMahon, 1992), failed to attract *Messor* ants in our study region, which is in accord with the results of previous studies on harvester ants (Gosselin et al., 2016; Csata and Dussutour, 2019). Activity of *Messor* ants can help restoration practices to develop palatable species in arid ecosystems. de Almeida et al. (2020) also emphasized the

important role of *Messor* ants in recruiting arid grassland through improving plant and soils.

5 Conclusions

The impacts of the activities of ants on plant communities were indirectly investigated by assessing the changes in plant community composition and structure in arid ecosystems. Ant activities increased heterogeneity in the plant communities through their nesting behaviors in creating distinct islands. The results of this study showed that desert ants had a positive effect on the dynamics of plant communities and could speed up the progress of succession in arid ecosystems. Ant-plant interactions varied depending on plant and ant species. Scavenger ants *Cataglyphis* and *Lepisiota* have increased invasive species in the area. These ants played an important role in enhancing the ecosystem potential for rehabilitation through seed bank preservation of pioneer and early-successional species. The activity of *Messor* ants was essential for the development and stability of climax in arid lands by seed bank preservation of late-successional and palatable species. Both harvester and scavenger ants play important roles in overcoming ecosystems against environmental stress such as drought through seed bank preservation. Desert ants can be considered as one of the most important drivers of ecological succession of plant communities and conservation of these ants diversity is crucial for the sustainability of arid ecosystems.

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